

Frogs of the *Hyla columbiana* Group: Taxonomy and Phylogenetic Relationships

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ABSTRACT. Three species comprise the *Hyla columbiana* group—*H. carnifex* on the Pacific slopes of Ecuador and the northern part of the Cordillera Central in Colombia, *H. columbiana* in the upper Río Cauca Valley in Colombia, and a new species, *H. praestans*, in the upper Río Magdalena Valley in Colombia. *Hyla variabilis* Boulenger, 1896, is placed in the synonymy of *H. columbiana* Boettger, 1892. The three species are readily distinguished by color pattern, morphometric features, and mating calls. The *Hyla columbiana* group belongs to a complex of Neotropical hylids characterized by 30 chromosomes and reduced larval mouthparts.

INTRODUCTION

Among the approximately 385 genera of Neotropical amphibians and reptiles, three—*Anolis*, *Eleutherodactylus*, and *Hyla*—contain more than 800 recognized species. These three megagenera represent a significant component of the entire Neotropical herpetofauna. The largest of these is the leptodactylid frog genus *Eleutherodactylus*, which contains approximately 360 species—115 in the West Indies, 70 in Middle America, and 175 in South America. The most widely distributed is the hylid frog genus *Hyla*; although most of the 230 species are Neotropical, including six in the West Indies, there are also 20 species in the Holarctic Realm. The 230 species of the

iguanaid lizard genus *Anolis* are divided about equally between the continental Neotropics and the West Indies; only one species is native to North America.

While we have attempted to sort out relationships among the hylid frogs during the preceding two decades, John D. Lynch has applied himself to *Eleutherodactylus*. Our current understanding of the taxonomy, relationships, and biogeography of the complex genus *Anolis* is largely the result of the assiduous efforts of Ernest E. Williams. In recognition of his devotion to the study of one of these megagenera and the frustrations associated with such endeavors, we dedicate this modest effort and a new species of *Hyla* to Ernest E. Williams.

Throughout the tropical lowlands of Middle and South America there are many species of small, yellowish-tan or brown *Hyla* that have pond-dwelling tadpoles with xiphicercal tails and reduced mouthparts. All of these species that have been studied karyologically have 30 chromosomes. There are few species of *Hyla* in the Andes, but some of these (*H. carnifex*, *H. columbiana*, and *H. variabilis*) resemble, superficially at least, the lowland taxa.

In 1975 we discovered a previously unknown species of small *Hyla* presumably related to *H. columbiana*. This find prompted our investigation of the taxonomy of the montane species and the definition of a *Hyla columbiana* group. In this paper we present the results of

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these studies and propose a phylogenetic arrangement of the group and its relatives.

MATERIALS AND METHODS

Systematic aspects of this study are based on the examination of 591 preserved specimens, 14 skeletons, 12 lots of tadpoles, and 1 clutch of eggs belonging to species in the *Hyla columbiana* group. Recordings were made on a Uher-4000 tape recorder and analyzed on a Vibralyzer (Kay Electric Company). All measurements of morphological features and calls were taken as described by Duellman (1970), and webbing formulae were ascertained following Savage and Heyer (1967). Tadpoles were staged according to Gosner's (1960) tables. Statistical analyses of morphometrics were based on measurements of uniformly preserved specimens from the vicinities of the type localities. Pairwise comparisons of measurements and proportions were accomplished by one-way analyses of variance (Sokal and Rohlf, 1969). Results of F_{\max} tests indicated normal distribution of the data. In a multiple comparison of the means, the Student-Newman-Keuls test was used to determine levels of significance.

All specimens are referred to by the following abbreviations: AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences, Philadelphia; BMNH = British Museum (Natural History); FMNH = Field Museum of Natural History; INDERENA = Instituto Nacional de Recursos Naturales, Bogota; KU = Museum of Natural History, University of Kansas; LACM = Museum of Natural History, Los Angeles County; MCZ = Museum of Comparative Zoology, Harvard University; NHMW = Naturhistorisches Museum, Wien; NHRM = Naturhistoriska Riksmuseet, Stockholm; SMF = Senckenberg Museum, Frankfurt-am-Main; UMMZ = Museum of Zoology, University of Michi-

gan; USNM = National Museum of Natural History; ZMB = Zoologisches Museum, Berlin; ZSM = Zoologisches Sammlung, München.

TAXONOMY

The *Hyla columbiana* Group

Definition. 1) Moderate sexual dimorphism in size; snout-vent lengths of males about 85% those of females; 2) snout short, blunt; 3) tympanum visible; tympanic annulus distinct or not; 4) hands and feet moderately webbed; 5) axillary membrane moderately extensive; 6) thoracic glands absent; 7) calcars and tarsal tubercles absent; ulnar tubercles present or absent; 8) males having single, median, subgular vocal sacs and no nuptial excrescences; 9) dorsum tan or brown, with or without dark dorsal markings and pale dorsolateral stripes; 10) pale labial stripe or spots present or not; 11) axilla and groin marked with yellow, orange, red or bluish gray in life; 12) anal, ulnar, and tarsal stripes absent; 13) iris bronze to reddish copper; 14) quadratojugal absent; 15) prevomers not articulating with maxillary arch, bearing small, posteromedially inclined dentigerous processes; 16) crista parotica poorly to moderately ossified; 17) zygomatic ramus of squamosal extending about one-third distance to maxillary arch; 18) pterygoid poorly developed, anterior ramus articulating weakly with unexpanded pars palatina of maxillary at level of midorbit; medial ramus widely separated from otic region of neurocranium; 19) sacral diapophyses moderately expanded (45–60°), anterior edge forming acute angle with longitudinal axis of body; 20) ilia lacking obvious crests; preacetabular angle obtuse; 21) tadpoles having ovoid bodies and xiphicercal tails with moderately deep fins barely extending onto body; 22) larval mouths terminal with two rows of small papillae ventrally, robust serrate beaks, and one upper and two lower rows

of denticles; 23) mating call consisting of short, moderately pitched notes, followed or not by shorter secondary notes; 24) diploid chromosome number 30.

Content. Three species, which may be identified by the following key:

1. Broad pale dorsolateral stripe present; groin bluish gray mottled with black in life *H. praestans*
 - Pale dorsolateral stripe absent; groin yellow, orange, or red in life 2
2. Small yellow spots on upper lip; venter bright yellow in life *H. carnifex*
 - No yellow spots on upper lip; venter creamy yellow in life *H. columbiana*

Distribution. Moderate elevations (975–2,580 m) on the Pacific slopes of the Cordillera Occidental in Ecuador and in the upper Río Cauca and Magdalena valleys and the northern part of the Cordillera Central in Colombia (Fig. 1).

Comment. The chromosome number is known only for *Hyla carnifex* (KU 173114), and tadpoles are known only for *H. carnifex* and *H. columbiana*. The populations from the northern part of the Cordillera Central, Colombia, are tentatively assigned to *H. carnifex*.

Following is an account of each of the species in the *Hyla columbiana* group. The results of the analyses of the morphometric data are presented in Table 1. For illustrations of the adult and larva of *H. carnifex*, see Duellman (1969).

Hyla carnifex Duellman

Hyla carnifex Duellman, 1969: 242 (Holotype.—KU 117993 from Tandapi, 1,460 m, Provincia de Pichincha, Ecuador); 1974: 7; 1977: 43.

Hyla bogerti Cochran and Goin, 1970: 261 (Holotype.—USNM 118731 from Medellín, Departamento de Antioquia, Colombia). Synonymy *fide* Duellman (1974: 7).

Hyla charlesbogerti Goin, 1970: 788 (Substitute name for *Hyla bogerti* Cochran and Goin, 1970). Synonymy *fide* Duellman (1974: 7).

Diagnosis. 1) Size small, snout-vent length in males 24.6 to 27.7 mm, in females 29.2 to 32.5 mm; 2) head short, 28.5 to 31.3% of snout-vent length; 3)

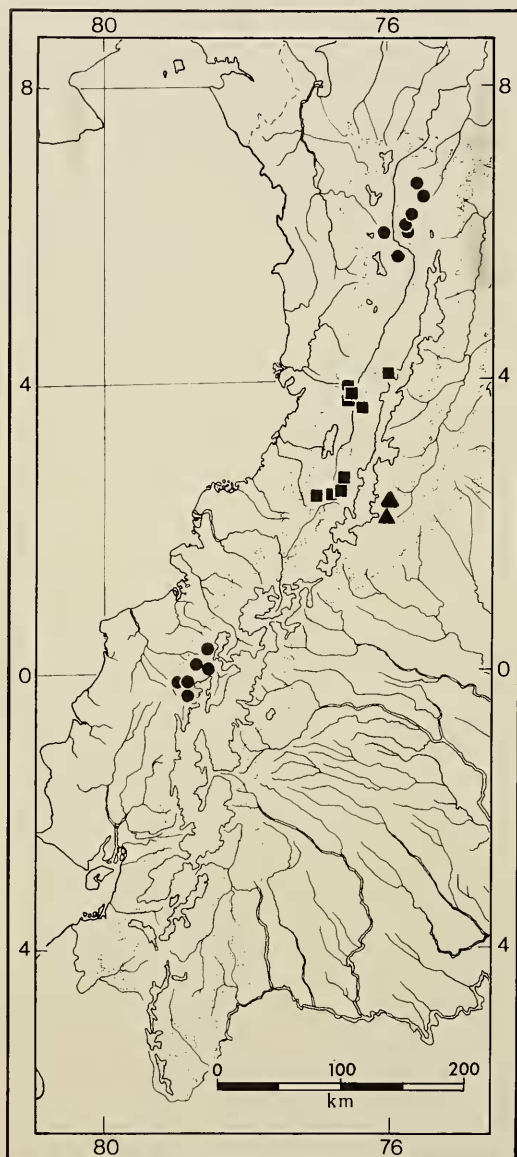


Figure 1. Western Colombia and Ecuador showing distributions of *Hyla carnifex* (●), *H. columbiana* (■), and *H. praestans* (▲). The dashed line is the 1,000-m contour; shaded areas are above 3,000 m.

snout round in profile; 4) interorbital distance narrow, 29.5 to 35.4% of head width; 5) skin on dorsum finely shagreened, nearly smooth; 6) ulnar tubercles distinct; 7) distal subarticular tubercle on fourth finger strongly bifid; 8) subanal tubercles

TABLE 1. STATISTICAL COMPARISON OF MORPHOMETRIC CHARACTERS OF TOPOTYPIC MALES OF THREE SPECIES IN THE *Hyla columbiana* GROUP.

First line = mean \pm 1 standard deviation; second line = observed range. Means of all characters of *H. columbiana* significantly different ($P < 0.05$) from those of the other species; significant differences ($P < 0.05$) between *H. carnifex* and *H. praestans* are indicated by an asterisk*.

Character	<i>H. carnifex</i>		<i>H. columbiana</i>		<i>H. praestans</i>	
N	20		20		8	
Snout-vent length (SVL)	26.1 \pm 0.90*	24.6 - 27.7	27.5 \pm 1.14	25.8 - 29.3	28.8 \pm 1.76*	26.0 - 31.5
Tibia/SVL	0.455 \pm 0.015	0.433 - 0.481	0.482 \pm 0.017	0.454 - 0.515	0.455 \pm 0.016	0.424 \pm 0.471
Foot/SVL	0.424 \pm 0.018	0.395 - 0.455	0.456 \pm 0.014	0.430 - 0.479	0.424 \pm 0.026	0.372 - 0.452
Head length/SVL	0.199 \pm 0.008	0.285 - 0.313	0.339 \pm 0.013	0.314 - 0.356	0.346 \pm 0.009	0.334 - 0.360
Head width (HW)/SVL	0.327 \pm 0.010	0.310 - 0.349	0.312 \pm 0.010	0.290 - 0.332	0.331 \pm 0.006	0.324 - 0.340
Interorbital/HW	0.332 \pm 0.015	0.195 - 0.354	0.416 \pm 0.032	0.358 - 0.471	0.319 \pm 0.021	0.300 - 0.347
Total prevomerine teeth	9.1 \pm 1.17*	7 - 11	7.3 \pm 1.13	6 - 10	8.6 \pm 1.51*	6 - 10

large; 9) dorsum tan with brown markings and usually with creamy yellow suborbital spot; 10) venter and vocal sac bright yellow, with or without brown spots on belly; 11) groin deep yellow orange; 12) mating call consisting of primary note followed by two or three secondary notes.

The presence of small, yellow spots on the upper lip and the bright yellow venter immediately distinguishes *H. carnifex* from other members of the group. Members of the *Hyla parviceps* group have larger suborbital spots and have white or gray venters and either orange spots on the ventral surfaces of the shanks or yellow spots on the anterior or dorsal surfaces of the thighs. The dorsal color pattern of *H. carnifex* resembles that of *H. minuta*, a species with a creamy yellow venter and white anal and heel stripes.

Description. Body robust; head small, noticeably narrower than body; snout short, its length about equal to diameter of eye, round in dorsal view and in profile; nostril about four-fifths distance from eye to tip of snout; canthus rostralis rounded, barely evident; loreal region slightly concave; lips moderately thick, not flared; internarial area noticeably

depressed; interorbital area slightly convex, much wider than eyelid; supratympanic fold short, moderately weak, obscuring upper part of tympanum; tympanic annulus indistinct; tympanum separated from eye by distance slightly greater than diameter of tympanum.

Axillary membrane short, extending about one-fourth length of upper arm; forearm moderately slender, bearing row of distinct ulnar tubercles; fingers short, fourth distinctly longer than second; discs round, half again as wide as digits; fingers webbed basally; webbing absent between first two fingers; webbing formula for other fingers II2-3-III3-2IV; subarticular tubercles moderately large, low, subconical; distal tubercle on fourth finger strongly bifid; supernumerary tubercles small, subconical, numerous on basal segments of digits; palmar tubercle flat, bifid; prepollical tubercle flat, elliptical; nuptial excrescences absent. Hind limbs moderately short, slender; calcars, tarsal folds and tubercles absent; inner metatarsal tubercle low, flat, elliptical; outer metatarsal tubercle evident in some specimens; toes moderately long, third and fifth subequal in length; toes about three-fourths webbed; webbing formula

II—(1½–2⁻) IIII—(1½–2⁻) IIII—(1⁻–2⁻) IV(2⁻–2—IV; subarticular tubercles small, round; supernumerary tubercles minute, present in single row on proximal segment of each digit.

Skin on dorsum weakly shagreened, nearly smooth; skin on throat, belly, and proximal posteroventral surfaces of thighs granular; skin on other surfaces smooth. Anal opening directed posteriorly at upper level of thighs; anal flap short; subanal tubercles large. Tongue elliptical, shallowly notched posteriorly, and barely free behind. Dentigerous processes short, posteromedially inclined, widely separated medially, between small ovoid choanae, bearing 3–4 to 5–6 teeth for totals of 7–11 (\bar{x} = 9.2, 20 ♂♂) and 4–5 to 6–6 teeth for totals of 9–12 (\bar{x} = 10.4, 15 ♀♀). Vocal slits short, extending from near midlateral base of tongue towards angles of jaws. Vocal sac large, single, median, subgular.

Coloration in preservative. Dorsum of head, body, and limbs dark brown or grayish brown with darker brown flecks; middorsal dark brown blotch extending from occiput or eyelids at least to sacral region in all females (30) and most males (83 of 100); venter cream with or without dark brown spots; variation in 100 males and 30 females—plain (68%, 27%), spots on posterior part of belly (24%, 50%), spots on belly and chest (8%, 13%), spots on belly, chest, and throat (0%, 10%) (Fig. 2). Flanks dark brown, usually enclosing cream lateral streak; groin mottled dark brown and cream; posterior thighs brown with longitudinal cream stripe; axilla, webbing, and spots on upper lip cream; variation in number of small spots on upper lip in 130 adults—none 6.9%, one 70.0%, two 17.7%, three 3.1%, four 2.3%.

Coloration in life. Dorsum of head and body pale creamy tan or grayish tan with median brown or grayish-brown blotch and numerous dark brown flecks; dorsal surfaces of limbs, exclusive of thighs, pale brown with or without faint darker brown transverse bars; upper lip brown, usually with small yellow spots, at least

one below eye; axilla, posterior flanks, and anterior and posterior surfaces of thighs deep yellow or orange bordered by dark brown or black; ventral surfaces of shanks, inner surfaces of feet, webbing, and ventral surfaces of upper arms deep yellow or orange (deepest colors only in larger individuals; webbing orange-red in some large females); throat, belly, and median part of flanks bright yellow with or without faint brown, lavender, or gray spots; iris gray, flecked with reddish bronze.

Tadpoles. The tadpoles were described and illustrated by Duellman (1969). In structure and coloration they are much like those of *H. columbiana* (described and figured herein), except that the upper beak has distinct lateral processes and white flecks are absent on the body and tail.

Mating call. The mating call of *Hyla carnifex* consists of a monophasic primary note followed by two or three shorter secondary notes—"Wraah-ack-ack." Analysis of recordings of two individuals shows that call groups are repeated at a rate of about 14 calls per minute. Primary notes have durations of 0.20 to 0.36 sec. The fundamental frequency is at about 500 Hz, and the dominant frequency is the fifth or sixth harmonic at about 2,500 or 3,000 Hz (Fig. 3).

Distribution. This species is definitely known from the Pacific slopes of the Cordillera Occidental in Ecuador, where it occurs at elevations of 1,140 to 2,150 m. Northern populations assigned to this species are known from elevations of 1,480 to 2,580 m in the northern part of the Cordillera Central and the eastern slopes of the Cordillera Occidental in Departamento de Antioquia, Colombia (Fig. 1).

Remarks. The status of the populations in northern Colombia named as *Hyla bogerti* by Cochran and Goin (1970) and recognized as *H. carnifex* by Duellman (1974) is questionable. Although many specimens are available from Departamento de Antioquia, Colombia

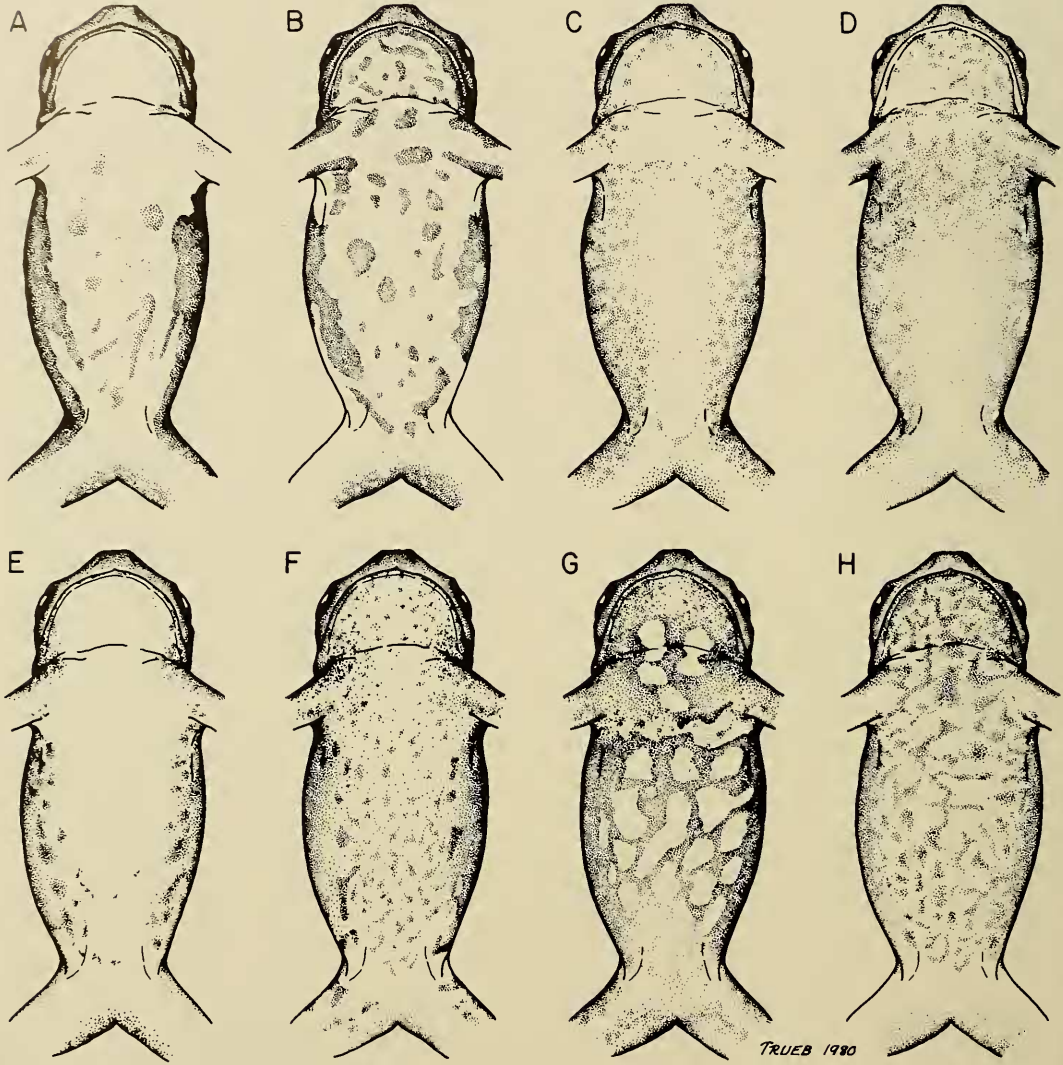


Figure 2. Ventral color patterns. *Hyla carnifex*: A. KU 164301, ♂. B. KU 164238, ♀. *Hyla praestans*: C. KU 169578, ♂. D. KU 169575, ♂. *Hyla columbiana*: E. KU 169470, ♂. F. KU 169490, ♂. G. KU 181165, ♂. H. KU 169472, ♀.

mento de Antioquia, Colombia, most are faded and poorly preserved, thereby making detailed morphometric comparisons useless. We have seen only one living specimen from Antioquia, and it had the distinctive bright yellow venter and flank pattern of *H. carnifex* from Ecuador. Although a gap of nearly 700 km separates the Ecuadorian localities from

those in Colombia, we anticipate that the species will be discovered along the intervening Pacific slopes of the Cordillera Occidental in Colombia. Until series of fresh, well-preserved specimens and recordings of mating calls are available from localities in northern Colombia, we can say only that living frogs from the widely separated regions have the same

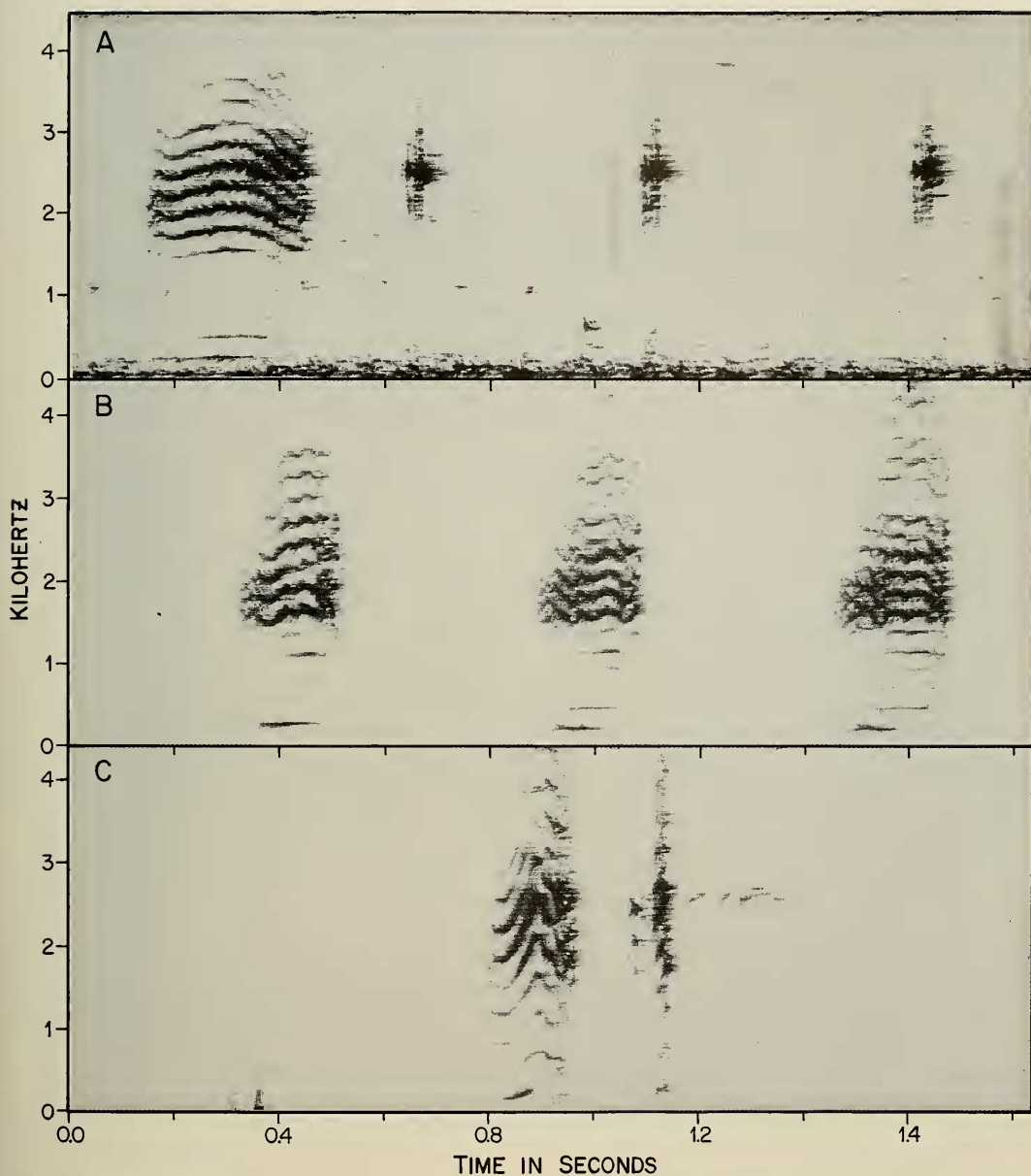


Figure 3. Audiospectrograms of mating calls of: A. *Hyla carnifex* (KU Tape 1237, 19°C). B. *H. columbiana* (KU Tape 1337, 17°C). C. *H. praestans* (KU Tape 1348, 17.5°C). Narrow band (45 Hz) analysis.

distinctive coloration; therefore, we assign them to the same species.

Only a few specimens of *H. carnifex* have been found by day—under the bark of logs, in bromeliads, and in axils of

leaves of elephant-ear plants (*Xanthosoma*). Calling males have been found between January and September. Males call from low (<50 cm), emergent herbs and grasses in marshy, temporary pools

in clearings in cloud forest. Tadpoles have been found in these pools from April to July, and metamorphosing young have been collected from May until August. Five young with tail stubs of <2 mm from Tandapi, Ecuador, collected on 18 July 1970, have snout-vent lengths of 12.7 to 14.7 (\bar{x} = 13.8) mm. Three young collected on 3 April 1975, 5 km east-southeast of Chiriboga, Ecuador, have snout-vent lengths of 15.0 to 15.5 (\bar{x} = 15.3) mm, and four obtained on 11 May 1975 at the same locality have snout-vent lengths of 16.1 to 18.2 (\bar{x} = 16.9) mm. In recently metamorphosed young, the dorsum is tan with a bronze tint; the anterior and posterior surfaces of the thighs and ventral surfaces of the shanks are dark gray, and the throat and belly are grayish white. In half-grown individuals (20–22 mm) the belly is white with a faint tint of yellow on the chin and chest; the flanks and anterior and posterior surfaces of the thighs are dark brown. A middorsal dark blotch is evident in these individuals, but the bright yellow or orange colors on the limbs and in the axilla and groin, and the spots on the upper lip do not develop until the frogs attain sexual maturity (snout-vent lengths of >23 mm in males and >27.5 mm in females).

Hyla columbiana Boettger

Hyla columbiana Boettger, 1892: 41 (Lectotype.—SMF 2365 [designated by Mertens, 1967: 4] from Popayán, Departamento de Cauca, Colombia); Nieden, 1923: 261; Cochran and Goin, 1970: 264; Duellman, 1977: 48.

Hyla variabilis Boulenger, 1896: 20 (Syntypes.—BMNH 1947.2.13.15–21; FMNH 3565; MCZ 2606; UMMZ 46464, 51269, 58908 [8 specimens]; USNM 71115 from Cali, Departamento de Valle, Colombia); Nieden, 1923: 262; Cochran and Goin, 1970: 258; Duellman, 1977: 108. NEW SYNONYMY.

Diagnosis. 1) Size small, snout-vent length in males 25.8 to 29.3 mm, in females 30.6 to 35.4 mm; 2) head moderately long, 31.4 to 35.6% of snout-vent length; 3) snout round in profile; 4) interorbital distance wide, 35.8 to 47.1% of

head width; 5) skin on dorsum smooth with scattered, small tubercles; 6) ulnar tubercles low, indistinct; 7) distal subarticular tubercle on fourth finger weakly bifid; 8) subanal tubercles small; 9) dorsum tan with brown markings; 10) venter creamy yellow with variable amount of brown or black markings (flecks to reticulations); vocal sac bright yellow in life; 11) groin yellow-orange to tomato-red in life; 12) mating call consisting of groups of 2 to 6 notes of equal duration.

The combination of small tubercles on the dorsum and absence of distinct labial spots and dorsolateral stripes distinguishes *H. columbiana* from other members of the group. The deep yellow, orange, or red axilla and groin and the extensive flecking or reticulations on the venter distinguish *H. columbiana* from all other species of small Neotropical *Hyla*.

Description. Body moderately robust; head as wide as body; snout moderately long, half again length of eye, round in dorsal view and in profile; nostril about two-thirds distance from eye to tip of snout; canthus rostralis acutely rounded; loreal region barely concave; lips thick, not flared; internarial area slightly depressed; interorbital area flat, nearly twice width of eyelid; supratympanic fold moderately weak, curving posteriorly, obscuring upper edge of tympanum; tympanic annulus distinct; tympanum separated from eye by distance only slightly greater than diameter of tympanum.

Axillary membrane moderately long, extending about two-fifths length of upper arm; forearm moderately robust; ulnar tubercles low, indistinct; fingers short, fourth slightly longer than second; discs round, slightly wider than digit; fingers webbed basally; webbing absent between first two fingers; webbing formula for other fingers II2⁻—3—III2½—2IV; subarticular tubercles small, subconical; distal tubercle on fourth finger weakly bifid; supernumerary tubercles small, subconical, numerous on basal segments; palmar tubercle low, flat,

weakly bifid; prepollical tubercle flat, elliptical; nuptial excrescences absent. Hind limbs moderately long, slender; calcars, tarsal folds and tubercles absent; inner metatarsal tubercle flat, narrowly elliptical; outer metatarsal tubercle absent; toes moderately long, third and fifth subequal in length; toes about three-fourths webbed; webbing formula $I(1-1\frac{1}{2})-2III1\frac{1}{2}-(2-2+III(1+1\frac{1}{2}))-2IV2-(1-1+V)$; subarticular tubercles small, subconical; supernumerary tubercles minute, subconical, numerous on proximal segments of each digit.

Skin on dorsal surfaces of head, body, and limbs smooth with scattered, small tubercles; skin on throat, belly, and proximal posteroventral surfaces of thighs coarsely granular. Anal opening directed posteriorly at upper level of thighs; anal flap short; subanal tubercles small. Tongue ovoid, barely notched behind, only slightly free posteriorly. Dentigerous processes of prevomers small, posteromedially inclined, moderately separated medially, between posterior borders of small, ovoid choanae, bearing 3-3 to 5-5 teeth for totals of 6-10 ($\bar{x} = 7.3$, 20 ♂♂) and 4-5 to 6-7 teeth for totals of 9-13 ($\bar{x} = 11.0$, 3 ♀♀). Vocal slits long, extending from midlateral base of tongue to angles of jaws. Vocal sac large, single, median, subgular.

Coloration in preservative. Dorsal surfaces of head, body, and limbs tan to brown with three types of patterns of darker brown markings in 40 recently preserved specimens: 1) middorsal blotch extending from eyelids to middle of dorsum and a smaller blotch usually evident in sacral region (50%); 2) narrow, diffuse stripe middorsally (25%); and 3) irregular flecks and/or reticulations (25%). Dorsal surfaces of limbs plain, flecked, or barred (in some specimens having dorsal blotches). Pale canthal, labial, and dorsolateral stripes absent; faint dark canthal and postorbital stripes evident in some specimens. Venter creamy tan with a variable amount of flecking and reticulation in 40 specimens (Fig. 2): 1) no flecks (35%); 2) flecks and reticulations

only in groin (30%); 3) reticulations in groin; flecks on belly, especially posteriorly (20%); and 4) reticulations in groin and on belly (15%). All females and some males in last category; females also having reticulations on throat. Anterior and posterior surfaces of thighs brown or tan with or without irregular brown markings; webbing and discs brown.

Coloration in life. At night dorsum yellowish tan; axilla, groin, proximal anterior surfaces of thighs, and inner surfaces of shanks pink to orange or yellow. By day, dorsum yellow, bronze, tan, or brown, with or without distinct brown blotches; venter yellow, with or without dark brown flecks and/or reticulations on belly; axilla, groin, proximal anterior surfaces of thighs, and inner surfaces of shanks deep yellow, orange, or red. Iris reddish copper. In some individuals, a faint dark canthal stripe and a dark brown postorbital stripe extending onto the anterior flanks are present; also, in some individuals a diffuse creamy yellow suborbital bar is present (Fig. 4).

Tadpoles. Among a series of tadpoles (KU 170202) in developmental stages 25 through 41, a typical tadpole in stage 38 is described. Body length 13.2 mm; total length 35.5 mm; body as wide as deep, sides nearly parallel for most of the length of body posterior to eyes, deepest posteriorly; snout in dorsal view broadly rounded, in profile more acutely rounded; eyes large, directed laterally; nostril about midway between eye and tip of snout, directed anteriorly; spiracle sinistral, directed posterodorsally just below midline at point about two-thirds length of body; anal opening dextral. Caudal musculature moderately robust anteriorly, tapering to attenuated point posteriorly; fins deepest at about mid-length of tail, tapering abruptly to xiphicercal tail; depth of either fin at mid-length of tail about equal to depth of caudal musculature; dorsal fin barely extending onto body (Fig. 5).

Mouth small (about one-fourth greatest width of body), terminal, directed anteroventrally; upper lip bare; two rows of

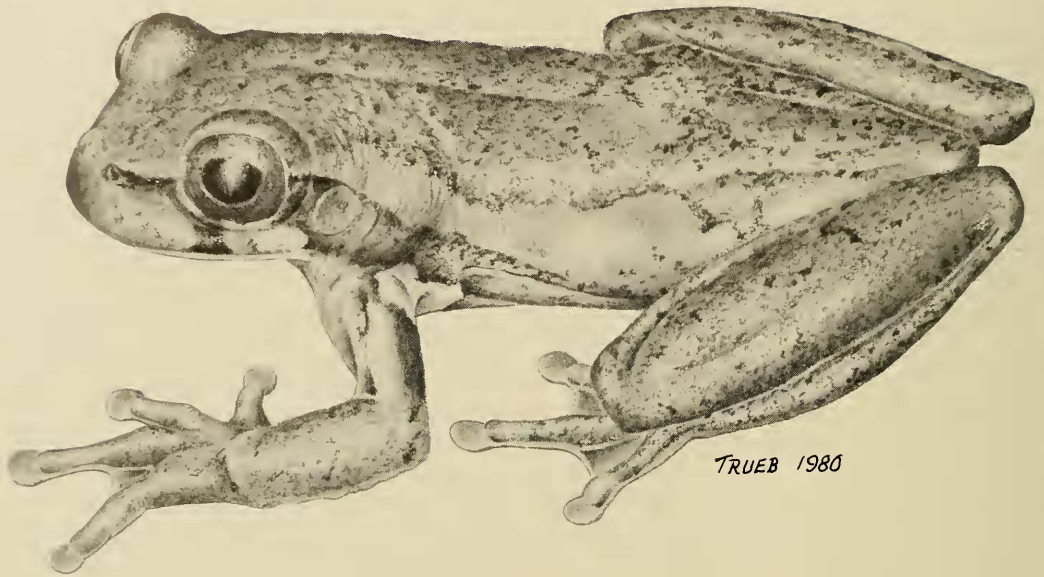


Figure 4. *Hyla columbiana*, KU 169463, ♂, 28.1 mm snout-vent length.

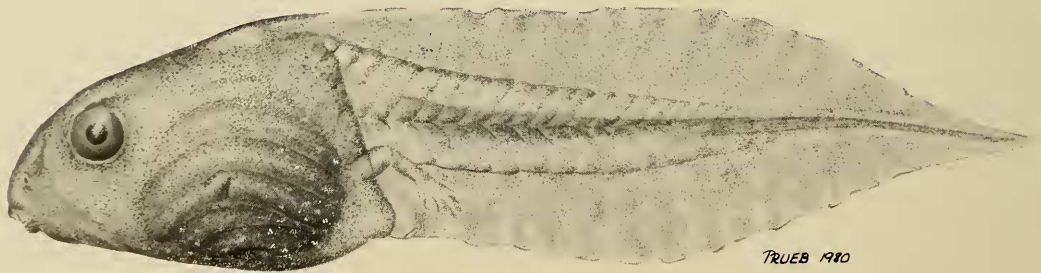


Figure 5. Tadpole of *Hyla columbiana*, KU 170202, 35.5 mm total length.

small, pointed papillae laterally and ventrally; lateral labial folds absent; beaks moderately massive, bearing fine serrations; upper beak broadly arch-shaped with no narrowed, lateral processes; lower beak broadly V-shaped; one upper and two lower complete rows of denticles; upper row just inside upper lip; second lower row having smallest denticles.

In preservative, dorsum of body and snout dull brown; sides and venter transparent with bluish sheen and numerous white flecks; caudal musculature orange-tan; caudal fins translucent; caudal musculature and fins bearing minute white flecks; in larger specimens (stage 30 and beyond), brown blotches on caudal fins, becoming larger and darker in larger tadpoles. In life, dorsum olive-

green with broad, tan dorsolateral stripe; tail cream with minute brown flecks in small individuals and brown spots on fins in larger individuals; venter silvery white; iris pale bronze.

Mating call. The mating call of *Hyla columbiana* consists of short series of similar notes. Analysis of recordings of five individuals reveals that each call consists of groups of 2 to 6 (\bar{x} = 3.6) notes repeated at a rate of 12 to 16 (\bar{x} = 14.4) notes per minute. Each note has a duration of 0.1 to 0.3 (\bar{x} = 0.16) sec. The fundamental frequency is at 240 to 320 (\bar{x} = 265) Hz. The eighth or ninth harmonic is emphasized, giving a dominant frequency of 2,000 to 2,560 (\bar{x} = 2,480) Hz (Fig. 3).

Remarks. Examination of the type specimens of *Hyla columbiana* and *H. variabilis* and study of living and preserved specimens from the regions of the type localities of the two named taxa, as well as analyses of mating calls, reveal the presence of only one species in the upper Río Cauca Valley. Cochran and Goin (1970: 260, 266) noted colors of a few living specimens from Cali and Popayán; they emphasized that the axilla was red in specimens from Popayán and yellow in specimens from Cali. In a series of 38 adults collected 8 km east of Popayán, the color of the axilla varied from deep yellow to orange and tomato-red, in living frogs from Lago de Calima (north of Cali) the axilla was pink.

Notable ontogenetic, sexual, and geographic variation exists in the amount of dark pigmentation on the venter. Juveniles lack dark pigment ventrally, whereas large adult females of all populations have reticulate venters, a condition also seen in many males from Cali and a few males from Popayán (Fig. 2).

We have observed this species only in disturbed areas that formerly supported cloud forest. Three individuals were found in *Agave* plants by day. All others were in shallow, grassy marshes or pools at night. Males call from clumps of grass in water or from grasses within 5 cm of

the surface. On 20 September 1974 we found a single clutch of eggs attached to grass on the surface of the water in a temporary pool. Tadpoles were found in the same pool.

Five recently metamorphosed young (KU 170201) have snout-vent lengths of 13.7 to 18.6 (\bar{x} = 16.1) mm. In life, the dorsum was bronze tan; the anterior and posterior surfaces of the thighs were dark brown. The upper arms and suborbital bar were creamy yellow, and the throat and belly were white. The iris was reddish bronze. In preservative, the juveniles are pale tan dorsally and creamy white ventrally; there is no indication of flecks or reticulations on the belly or in the groin.

Distribution. *Hyla columbiana* is widespread in the upper Río Cauca Valley, Colombia, where it occurs on the valley floor at elevations of 975 to 1,000 m and on the lower eastern slopes of the Cordillera Occidental and western slopes of the Cordillera Central to elevations of 2,250 m. It also occurs in the upper drainage of the Río Patía, where it is known from elevations of 1,800 to 2,350 m (Fig. 1).

Hyla praestans new species

Holotype. KU 169575, an adult male, from the Parque Arqueológico San Agustín, 3 km southwest of the village of San Agustín, Departamento de Huila, Colombia (1°53'N, 76°16'W), 1,750 m, one of a series obtained on 27 May 1975 by William E. Duellman, John E. Simmons, and Linda Trueb.

Paratypes. KU 169574, 169576–80, MCZ 100216, INDERENA (2 specimens) collected with the holotype.

Referred Specimens. ICN 7556–58 from 7.4 km (by road) NW of San José de Isnos, Departamento de Huila, Colombia, 1,970 m (John D. Lynch, personal communication).

Diagnosis. 1) Size small, snout-vent length in males 26.0 to 31.5 mm, females 31.2 mm; 2) head moderately long, 33.4 to 36.0% of snout-vent length; 3) snout in profile truncate, rounded above; 4) interorbital distance narrow, 30.0 to 34.7% of head width; 5) skin on dorsum finely

shagreened, nearly smooth; 6) ulnar tubercles absent; 7) distal subarticular tubercle on fourth finger strongly bifid; 8) subanal tubercles small; 9) dorsum tan with creamy yellow labial stripe and orange-tan dorsolateral stripe; 10) venter and vocal sac creamy white with brown flecks on belly; 11) groin pale bluish gray mottled with black; 12) mating call consisting of primary note followed by one or two secondary notes.

Hyla praestans differs from the other members of the *Hyla columbiana* group by having pale labial and dorsolateral stripes; the latter is characteristic of females of many species in the *Hyla parviceps* group, all of which have yellow spots on the thighs or orange spots on the ventral surfaces of the shanks. Another distinguishing feature of *H. praestans* is the bluish-gray groin with black mottling, a pattern occurring in some populations of *H. labialis*, a much larger frog that is uniformly dark green dorsally.

Description. Body robust; head slightly narrower than body; snout moderately short, only slightly longer than diameter of eye, round in dorsal view, truncate and rounded above in profile; nostril about two-thirds distance from eye to tip of snout; canthus rostralis rounded; loreal region slightly concave; lips moderately thick, not flared; internarial area slightly depressed; interorbital area flat, much wider than eyelid; supratympanic fold short, weak, obscuring upper part of tympanum; tympanic annulus distinct; tympanum separated from eye by distance one third greater than diameter of tympanum.

Axillary membrane short, extending about one-fourth length of upper arm; forearm moderately slender, lacking ulnar tubercles; fingers moderately long, fourth slightly longer than second; discs round, slightly wider than digit; fingers webbed basally; webbing absent between first two fingers; webbing formula for other fingers $II2^-(3^--3^+)III3-2\frac{1}{2}IV$; subarticular tubercles moderately

large, subconical; distal tubercle on fourth finger strongly bifid; supernumerary tubercles low, flat; palmar tubercle low, flat, ovoid; prepollical tubercle flat, elliptical; nuptial excrescences absent. Hind limbs moderately long, slender; calcars, tarsal folds and tubercles absent; inner metatarsal tubercle small, flat, elliptical; outer metatarsal tubercle absent; toes moderately long, fifth barely longer than third; toes about two-thirds webbed; webbing formula $I2^--2III1-(2^--2)III(1-1\frac{1}{2})-2^--2)IV(2^--2\frac{1}{2})-(1-1\frac{1}{2})V$; subarticular tubercles small, subconical; supernumerary tubercles absent.

Skin on dorsum weakly shagreened, nearly smooth; skin on throat, belly, and proximal posteroventral surfaces of thighs weakly granular; skin on other surfaces smooth. Anal opening directed posteriorly at upper level of thighs; anal flap short; subanal tubercles small. Tongue elliptical, shallowly notched posteriorly, barely free behind. Dentigerous processes of prevomers small, posteromedially inclined, narrowly separated medially, between small, ovoid choanae, bearing 3-3 to 5-5 teeth for totals of 6-10 ($\bar{x} = 8.6$) teeth in males. Vocal slits long, extending from midlateral base of tongue to angles of jaws. Vocal sac large, single, median, subgular.

Coloration in preservative. Dorsal surfaces of head, body, and limbs brown with darker brown flecks on body and limbs and dark brown longitudinal streaks of variable size and distinctness on body. Narrow, cream to orange-tan canthal line from tip of snout to eye; broad, cream to orange-tan dorsolateral strip from eye to groin; flanks dark brown. Venter cream with variable amount of brown flecking or spotting on throat, belly, and thighs (Fig. 2); anterior and posterior surfaces of thighs creamy tan with dark brown mottling; webbing and discs brown.

Coloration in life. At night, dorsum tan with creamy yellow dorsolateral stripes. By day, dorsum and flanks dark brown with orange-tan dorsolateral stripes,

creamy tan canthal stripes, and creamy yellow labial stripe; groin mottled bluish gray and black; posterior surfaces of thighs dark brown; throat and belly creamy white with brown flecks; ventral surfaces of limbs tan; iris coppery brown (Fig. 6).

Measurements of holotype (in mm). Snout-vent length 28.3, tibia length 13.3, foot length 12.6, head length 9.8, head width 9.3, eye-nostril 2.5, interorbital distance 3.2, eyelid width 2.1, horizontal diameter of eye 2.8, horizontal diameter of tympanum 1.3.

Tadpoles. Unknown.

Mating call. The call of *Hyla praestans* consists of a primary note followed by one or two, shorter, secondary notes. Analysis of a single recording shows that the call groups are repeated at a rate of 4.5 calls per minute. The duration of the

primary note is 0.08 sec. The fundamental frequency is at 450 Hz, and the fifth harmonic at 2,250 Hz is dominant (Fig. 3).

Distribution. This species is known from elevations of 1,750 to 1,970 m on the lower eastern slopes of the Cordillera Central next to the upper Río Magdalena Valley, Colombia (Fig. 1).

Remarks. The region of the type locality is humid lower montane forest with bamboo, *Heliconia*, and some bromeliads. The exact type locality is a small, temporary pond immediately behind (± 100 m) the Museo Arqueológico San Agustín. Males were calling from a tangle of brambles over (up to 1 m above) the water at night following a light rain (13 mm).

Etymology. The specific name, *praestans*, is Latin meaning preminent or

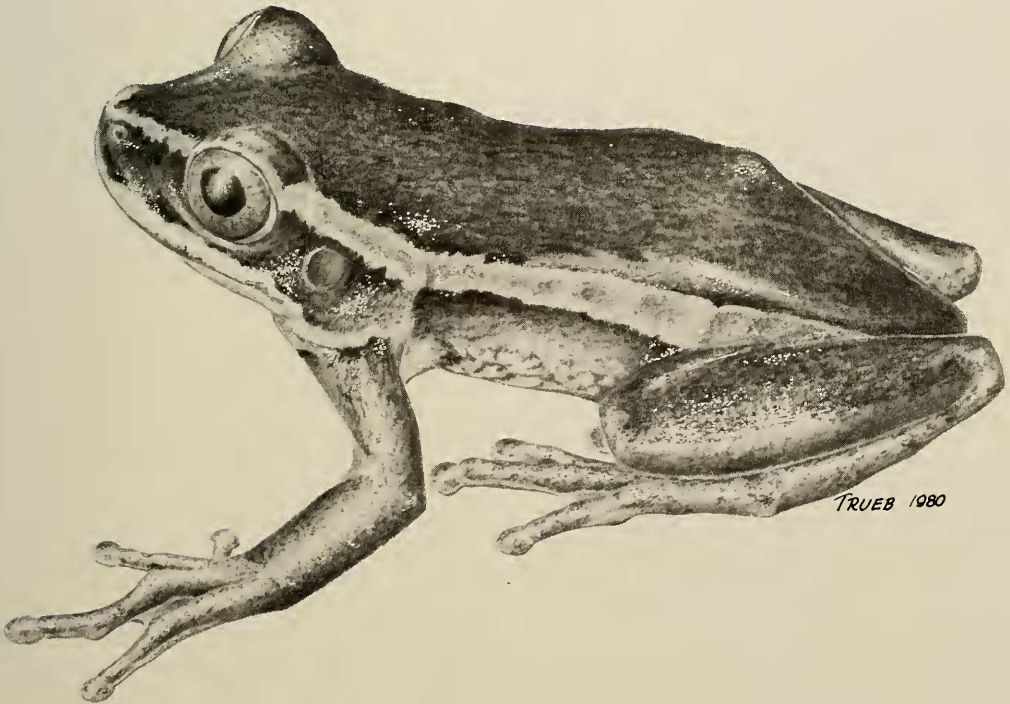


Figure 6. *Hyla praestans*, KU 169574, ♂, 27.3 mm snout-vent length.

distinguished and is proposed in recognition of Ernest E. Williams's recognized preeminence in the field of herpetology.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of groups of taxa may be inferred by determining shared-derived characters in defining monophyletic taxa; determination of sequential sets of shared-derived character states provides a stepwise association of character states defining branching sequences in a phylogenetic arrangement and classification reflecting these phylogenetic relationships. This approach has become known as phylogenetic systematics (see Wiley, 1980, for terms and methodology).

Although we can provide a reasonable hypothesis of the phylogenetic relationships of the *Hyla columbiana* group with other groups of *Hyla*, the distribution of character states among the species within the group and the absence of meaningful interpretation of evolutionary trends of many characters, such as skin texture and coloration, defies a reconstruction of the phylogeny of the three species. Using 10 of the characters listed in the diagnoses (all except snout-vent length and proportion of head width) plus six cranial characters (nature of frontoparietal fontanelle, degree of ossification of sphenethmoid, shape of parasphenoid alae, serration of coronoid, and amount of separation of prevomers and of palatines), we found that there was little concordance in shared character states. *Hyla carnifex* shares six states with *H. columbiana* and seven with *H. praestans*, which shares only three with *H. columbiana*. Thus, even a phenetic analysis reveals only that *H. columbiana* has more unique character states than either of the other two species.

Various apparently related groups of Neotropical hylid frogs have been defined as a matter of convenience by Bokermann (1964), Duellman (1970, 1974), and Duellman and Crump (1974).

Informally recognized assemblages of species include the *leucophyllata* (6 species), *marmorata* (4), *microcephala* (± 12), *minuta* (2), and *parviceps* (7) groups. For the purposes of the following discussion, we add *H. labialis* and the *columbiana* group.

In attempting to ascertain the phylogenetic relationships among these groups, we utilized eight character states; 2 from adults, 5 from larvae and the karyotype. These states were selected because they are ones in which we place confidence in our knowledge of phylogenetic trends within the Hylidae. Other characters are highly variable within, as well as between, groups, or are restricted to members of only one group; therefore, they are useless in determining intergroup relationships. The characters, their states, and direction of evolutionary change (0 = primitive state; 1 = derived state; 2 = secondarily or independently derived state) are as follows:

A. *Chromosome number*. Hylid frogs have diploid numbers of 22, 24, 26, 28, or 30 chromosomes. Bogart (1973) showed that the primitive number of chromosomes in leptodactylids, the presumed ancestors of hylids, is 26—a number occurring in phyllomedusine, some pelodyadine, and some amphignathodontine hylids. Most hylid frogs have 24 chromosomes, but all species so far examined of the groups of *Hyla* listed above have 30 chromosomes, a number unknown in other groups of hylids. Bogart (1973) and Morescalchi (1973) suggested that the evolution of 30 chromosomes occurred by centric fission, and Bogart (1973) noted variable numbers of pairs of telocentric chromosomes in those species having a diploid number of 30. Because this number is unique to the groups of *Hyla* under consideration, we assume that this chromosome number is a uniquely derived character state in these frogs. The coded character states and polarity are:

0 = <30 chromosomes; 1 = 30 chromosomes

0 \rightarrow 1

B. *Quadratojugal arch*. Primitively in anurans, the quadratojugal forms a complete arch between the quadrate and the maxillary. This bone is reduced or absent in a number of primitive and advanced families (Lynch, 1973), including some leptodactylids (Lynch, 1971) and some hylids (Duellman, 1970). The presence of a complete quadratojugal arch is primitive (Lynch, 1973; Trueb, 1973). The coded character states and polarity are:

0 = arch complete; 1 = quadratojugal reduced or absent

0 → 1

C. *Nuptial excrescences*. Nuptial excrescences on the prepollex of breeding males usually are associated with species that amplex in water, and the absence of excrescences is characteristic of those that amplex on land or on vegetation (Parker, 1940; Lynch, 1971). Presence of excrescences is considered to be primitive. The coded character states and polarity are:

0 = excrescences present; 1 = excrescences absent

0 → 1

D. *Larval body shape*. The general configuration of the body of tadpoles is a reflection of the major habitats in which they develop. Tadpoles in torrential streams tend to have depressed bodies, whereas those in ponds generally have ovoid bodies. Modifications of pond tadpoles are associated with the level in which they feed in the water column; both surface-feeders and bottom-feeders are more depressed in comparison with midwater-feeders. In dorsal view, tadpoles of the *Hyla leucophyllata* group have a lateral constriction at midbody, resulting in a violin shape. The coded character states and polarity are:

0 = ovoid; 1 = violin; 2 = depressed

0 → 1; 0 → 2

E. *Larval tail shape*. The tadpoles of most frogs in primitive and advanced families have a tail that terminates in a rounded or acuminate tip; the caudal musculature terminates anterior to the margin of the fin. In some of the hylids under consideration, the caudal muscula-

ture extends posterior to the margin of the fins, which extend as a narrow fringe along the terminal part of the musculature. This type of tail with a distal filament is termed xiphicercal and is a derived feature. The coded character states and polarity are:

0 = acute; 1 = xiphicercal

0 → 1

F. *Larval mouth position*. The generalized tadpole mouth is directed anteroventrally. Stream-adapted tadpoles have ventral mouths, and surface-feeding tadpoles have mouths directed dorsally. Some midwater tadpoles have mouths directed anteriorly at the tip of the snout. The coded character states and polarity are:

0 = anteroventrally; 1 = anteriorly

0 → 1

G. *Larval labial papillae*. In pond-dwelling tadpoles of the Leptodactylidae and Hylidae, the mouth usually is bordered ventrally by two rows of small papillae. Within the groups under consideration, we find one or two rows of small papillae, one row of large papillae, or no papillae. The large papillae seem to represent a fusion of smaller papillae, and the absence of papillae seems to result from the fusion of large papillae into a dermal fold, as seen laterally in members of the *Hyla parviceps* group. The coded character states and polarity are:

0 = 2 small rows; 1 = 1 small row;

2 = 1 large row; 3 = none

0 → 1; 0 → 2 → 3

H. *Larval labial denticles*. The standard denticle formula in tadpoles is two upper rows and three lower rows (2/3). This number is increased in many stream-adapted tadpoles and to a lesser extent in some pond-dwelling tadpoles. Within the Hylidae reduction of the number of rows of denticles is uncommon in free swimming and feeding tadpoles and is most extreme in the groups considered here. The coded character states and polarity are:

0 = 2/3; 1 = 1/2; 2 = 0/1; 3 = 0/0

0 → 1 → 2 → 3

In order to ascertain the evolutionary

trends within the groups being considered, it is necessary to have an outgroup for comparison. Ideally such an outgroup should be the most closely related taxon, but such a determination is not presently possible because of our inadequate knowledge of many Neotropical hylids. Thus we have chosen to make the comparisons with *Smilisca*, a genus of six generalized species of Neotropical hylids (Duellman and Trueb, 1966). The character states for the taxa are given in Table 2, and the resulting phylogenetic arrangement is shown in Figure 7.

Thus, if our assumption that the presence of 30 chromosomes defines a monophyletic complex of hylid frogs is correct, then it is evident that the major evolutionary trends in this complex involve larval structure, especially mouthparts. Wassersug (1980) emphasized that larval buccal morphology in the *Hyla leucophyllata* group was specialized for macrophagy and that this specializaion

was best developed in the *Hyla microcephala* group. The ecological and biogeographical significance of these modifications are not well understood. In those few species that have been studied (Crump, 1974; Duellman, 1978), the reproductive strategy is to deposit multiple clutches of small eggs in, or on, vegetation above, temporary ponds.

Throughout most of the lowlands in tropical America, three or four species of this complex occur in sympatry, but 11 species occur sympatrically in Amazonian Ecuador. Only two of the groups occur in the Andes. The three species of the *Hyla columbiana* group have allopatric distributions in the western and central cordilleras in Colombia and Ecuador, whereas *Hyla labialis* inhabits higher elevations (2,400–3,000 m) in the Cordillera Oriental in Colombia and the Mérida Andes in Venezuela. The diversity of species in this complex in the tropical lowlands may be the result of

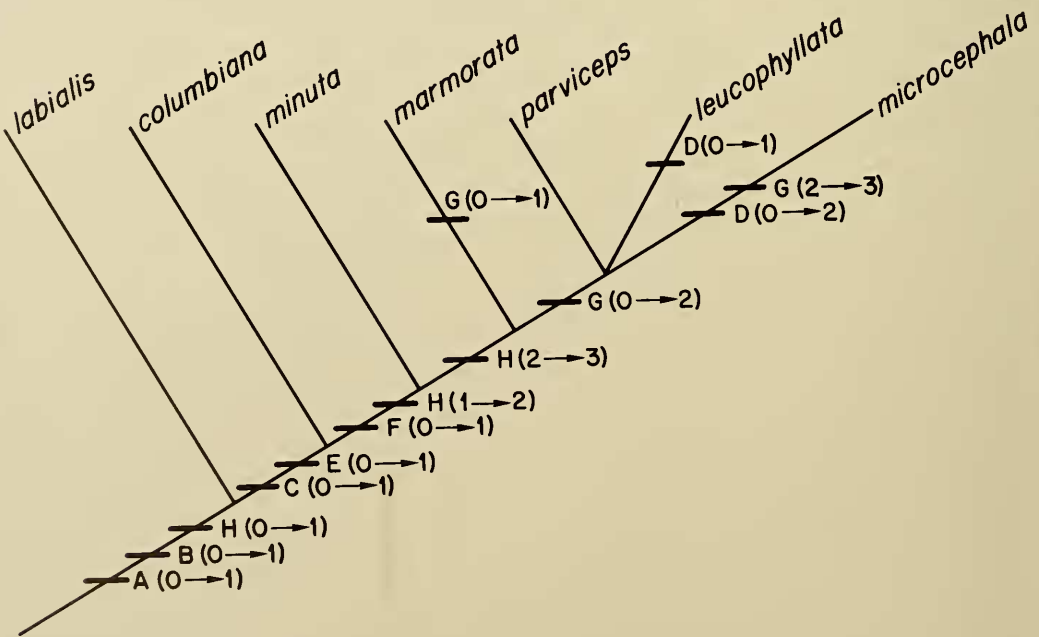


Figure 7. Reconstruction of the phylogeny of groups of Neotropical *Hyla* with 30 chromosomes. Shifts in character states are indicated by the horizontal bars and identified by the letters and numbers given in Table 2 and text.

TABLE 2. CHARACTER STATES OF GROUPS OF *HYLA* HAVING 30 CHROMOSOMES.

Group	Characters							
	A	B	C	D	E	F	G	H
<i>H. labialis</i>	1	1	0	0	0	0	0	1
<i>H. columbiana</i>	1	1	1	0	1	0	0	1
<i>H. minuta</i>	1	1	1	0	1	1	0	2
<i>H. marmorata</i>	1	1	1	0	1	1	1	3
<i>H. parviceps</i>	1	1	1	0	1	1	2	3
<i>H. leucophyllata</i>	1	1	1	1	1	1	2	3
<i>H. microcephala</i>	1	1	1	2	1	1	3	3
Outgroup (<i>Smilisca</i>)	0	0	0	0	0	0	0	0

late Cenozoic and Quaternary climatic-ecological fluctuations in the tropical lowlands that resulted in the alternating fragmentation and reunification of forest and nonforest habitats (Haffer, 1979; Duellman, 1982a). On the other hand, the allopatric distributions of the few species in the Andes may reflect isolation of previously more widespread species with the uplift of the Andes or as a consequence of the vicissitudes of Pleistocene climatic change in the Andes (Simpson, 1975, 1979; Duellman, 1979, 1982b).

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APPENDIX: SPECIMENS EXAMINED

Only specimens of the *Hyla columbiana* group are listed.

Hyla carnifex (427). COLOMBIA: *Antioquia*: Envigado, AMNH 39796, 39798–99; Finca San José de Bella Vista, LACM 47036–52, 47139; Jericó, 1,970 m, KU 98139–41, 98142 (skeleton), MCZ 15076–100, 24888–93, UMMZ 90601, USNM 118243; La Ceja, 2,180 m, FMNH 63883; Medellín, 1,480 m, AMNH 1357, ANSP 25005, FMNH 17098–101, MCZ 7664–65, UMMZ 56508 (38), 60251 (2), 92167, USNM 75989, 118729–31; Río Porce, ANSP 25773; San José de los Andes, LACM 72999; San Pedro de Osa, 2,450 m, AMNH 38713–14, 39153–77, ANSP 21029, FMNH 30567–69, 63884, 63897, MCZ 24911–15, UMMZ 71214, 71215 (2), 78301 (17), USNM 152021–29; Santa Rosa, 2,580 m, AMNH 39453, 39458, Yarumal, 2,265 m, USNM 152030–31. ECUADOR: *Azuay*: Cuenca (? locality), AMNH 23703, SMF 2368, ZMB 28023. *Imabura*: Apuela, 1,550 m, KU 117992, 132428–41, 132544 (tadpoles). *Pichincha*: 5 km ESE Chiriboga, 2,010 m, KU 164302–05, 166189–92, 166311–14 (skeletons), 173113–15; 4 km W Chiriboga, 2,120 m, KU 142638–44; 14 km W Chiriboga, 1,960 m, KU 164306–07, 166193–95 (tadpoles); 4 km NE Dos Ríos, 1,140 m, KU 164283–301, 166188 (tadpoles); Hwy 28, 22 km from Hwy 30, 1,770 m, MCZ 91202; Milligal (? = Milligalli), USNM-GOV 8041–47; 3.5 km NE Mindo, 1,540 m, KU 164308–11; Tandapi, 1,460 m, AMNH 81399–403, BMNH 1969.640–44, FMNH 170746–50, KU 109557 (skeleton), 111838–66, 111867–70 (skeletons), 111871–90, 112360 (tadpoles), 117993–8001, 132442, 136199–254, 138775–76 (tadpoles), 178720–22, 180352 (tadpoles), MCZ 75062–66, UMMZ 129016 (8), USNM 166543–50; 6.3 km E Tandapi, 1,770 m, MCZ 94728; 9 km SE Tandayapa, 2,150 m, KU 164312.

Hyla columbiana (180). COLOMBIA: *Cauca*: El Tambo, 1,800 m, ANSP 25148, FMNH 54776, KU 145075–79, NHRM 2015 (11); road to Munchique, 2,350 m, KU 148493 (tadpoles); Popayán, 1,740 m, ANSP 25677, FMNH 43933–80, 43982–91, 44050, 44109, 82005–07, SMF 2365, USNM 152081–82, 152146–51; 8 km E Popayán, 2,110 m, Inderena (2), KU 169464–98, 170110–12 (skeletons), 170201–02 (tadpoles), 170203 (eggs); Quintana, FMNH 54719; 4 km S Silvia, 2,200 m, KU 169461–62; 6 km S Silvia, 2,250 m, KU 169463. *Quindío*: Boquía, 25 km N Armenia, 1,710 m, KU 133449, 139524. *Valle*: Cali, 1,000 m, AMNH 10674–77, BMNH 1947.2.13.15–21, FMNH 3565, MCZ 2606, NHMW 6198, 19438, SMF 2642–44, UMMZ 46464, 51269, 58908 (8), USNM 71115, ZSM 1182/0 (3); Candelaria, 975 m, USNM 151983–84; Cerro La Herrera, USNM 137770–72;

Finca Wesfalia, ZSM 315/1937; Lago de Calima, 1,350 m, KU 181165-66.

Hyla praestans (11). COLOMBIA: *Huila*: Parque Arqueológico San Agustín, 3 km SW San Agustín, 1,750 m, INDERENA (2), KU 169574-80, 170113 (skeleton), MCZ 100216.

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